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# Diversity and differentiation of the *Chelonus* (*Microchelonus*) species of the Galapagos archipelago (Hymenoptera, Braconidae, Cheloninae)

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## Abstract

Despite the significance of the Galapagos archipelago, the richness of diverse groups such as braconid wasps remains poorly studied. Seven species of chelonine Braconidae are recorded for the Galapagos islands for the first time: *Chelonus buscki* Viereck, 1912, *Chelonus carinatus* Provancher, 1881, *Chelonus johni* Marsh, 1979, *Chelonus refluus* (Papp, 2010), *Chelonus sulcifera* (Papp, 2016), *Chelonus topali* (Papp, 1999), and *Chelonus turgoclarus* (Papp, 2010). No endemic species were identified for the islands. We also explore island population differences with respect to island area, age, and distance between islands. The populations of *C. buscki* and *C. carinatus* were statistically differentiated between islands. Morphological differences were associated with island area only for *C. buscki* while no relationship was found between differentiation and age or geographic distance between islands for any species. These results could be a consequence of recent colonization events.

## Keywords

Island biogeography, morphological differentiation, parasitoid, proportions spectrum analysis

## Introduction

Archipelagos are isolated island systems that can evolve as different environmental units from continental masses (Santamarta 2016). Archipelagos can be blank slates for species colonization and diversification depending on the age, distance from mainland areas, and other characteristics of the islands (Parent et al. 2008; Losos and Ricklefs 2009). The standard colonization process assumes that when the first migratory species arrive, abundant niches are available on the islands (Mayr 1965; Emerson 2008). Then, the number of species increases through speciation and immigration, at a rate dependent on isolation and time (Mayr 1965; Gillespie and Roderick 2002; Emerson 2008). Along with these changes, the phenotypic differentiation between the members of a clade, being either sympatric or allopatric, may occur as species adapt to use different resources (Mayr 1965; MacArthur and Wilson 1967; Rundle and Nosil 2005; Losos and Mahler 2010; Dudaniec et al. 2011).

This process of colonization and differentiation of populations from the oldest to the youngest of islands was described as the rule of progression (Funk and Wagner 1995; Hennig 1966; Poulakakis et al. 2020), and gives an important role to the age of the islands in causing the diversification of the species (Gillespie and Roderick 2002) with numerous examples in archipelagos such as Hawaii (Roderick and Gillespie 1998). However, the expected relationship between differentiation of the founding populations and island age may be altered by events such as the time of arrival of the founding species, its biology, and the geographical complexity of the archipelago (Sequeira et al. 2002; Hormiga et al. 2003; Bonacum et al. 2005; Kvist et al. 2005; Schmitz et al. 2007; Haines et al. 2014). In the case of parasitoid species, such as chelonine wasps, successful colonization depends on prior colonization by suitable host insect species.

For the Galapagos islands, as for practically all the planet, arthropods represent most of the natural terrestrial biodiversity (Peck 1997), indeed, a revision of literature indicates that little more than 2,000 species of insects have been documented for the archipelago, with a high level of endemism (Roque-Albelo L. 2008; Bungartz et al. 2012; Toral et al. 2017; Buchholz et al. 2020). An early inventory of the insects of the archipelago revealed that 47% of the species are endemic (Peck 1997; Peck et al. 1998), suggesting frequent events of early colonization and separation from their continental ancestors (Tye et al. 2002), favoring phenotype differentiation, this being one of the first steps to speciation (Grant et al. 2000; Yamaguchi and Iwasa 2013). However, few detailed studies about the diversification processes of the group in the islands have been conducted (Tye et al. 2002) with most papers focused on survey data.

Cheloninae is one of the largest subfamilies of Braconidae with more than 1,500 valid taxa (Yu et al. 2005; Dong et al. 2019). Despite their great species diversity, chelonines are easily recognized from most other braconids by their rigid, sculptured metasomal carapace, with the other parts of metasoma usually being concealed ventrally (Shaw 1983, 1997, 2006; Dadelahi et al. 2018; Ghahari et al. 2022). Chelonine wasp species are mostly solitary koinobiont egg-larval endoparasitoids of concealed Lepidoptera, especially attacking host species in the Tortricoidea and Pyralidoidea (Shenefelt 1973; Yu et al. 2005; Stireman and Shaw 2021). Chelonines are considered

economically important as biocontrol agents for suppressing plant-feeding caterpillars, especially those in the families Noctuidae, Geometridae, Tortricidae, Pyralidae, and Gelechiidae (Shaw and Huddleston 1991). However, despite their importance to biological control programs only about a quarter of the chelonine wasp species have been described and many are poorly characterized, making their recognition to species level difficult (Aydogdu and Beyarslan 2011).

There is debate regarding the treatment of some genera within Cheloninae. *Microchelonus*, for example, is considered as a subgenus within *Chelonus* by some authors (McComb 1968; Shaw 1991, 1997, 2006; Nascimento and Penteado-Dias 2011; Sharkey et al. 2021; Ghahari et al. 2022; Ranjith and Priyadarsanan 2023). However, some authors have treated *Microchelonus* as a valid genus, close to *Chelonus* (Tobias 1995, 2001, 2008, 2010; Chen and Ji 2002; Papp 2016). Papp (1995) mentions that *Microchelonus* always has 16 antennomeres and a foramen in the apical part of the carapace of males while *Chelonus* is characterized by a variable number of antennomeres and the absence of the apical foramen. The species treated in this paper can all be assigned to the *Chelonus* subgenus *Microchelonus*.

In this study, we explore the morphological differentiation in the populations of the seven known species of *Chelonus* (*Microchelonus*) in the Galapagos Islands. We explore the above-described expectations of evolutionary processes by considering the following hypotheses: 1. Each island of the Galapagos archipelago hosts different species of the genus *Chelonus*, 2. There is a direct relationship between island age and morphologic variation in populations of *Chelonus*, 3. If present, the degree of differentiation between species or populations of *Chelonus* on each island is associated with the age of the islands, 4. If present, the degree of differentiation between species or populations of *Chelonus* on each island is associated with the geographical proximity between the islands.

# Methods

## Study area and sampling

A total of 114 specimens of *Chelonus* were studied from the following islands of Galapagos archipelago: Floreana, Pinta, San Cristobal, Isabela, Santiago, Fernandina, Española, and Santa Cruz. Voucher specimens from this study are deposited at the Entomology Museum of the Facultad de Recursos Naturales, of the Escuela Superior Politécnica de Chimborazo, Riobamba, Ecuador, and the Terrestrial Invertebrates Collection of the Charles Darwin Research Station, Galapagos, Ecuador (ICCDRS). The specimens were obtained through a standardized survey carried out in the Galapagos Islands from 2017 to 2021. This consisted in the use of three collection methods with standard effort units: four runs of 50 double sweep nets, five pan traps separated by 5 m and left for 72 hours, and finally three Malaise traps separated by 50 m and left for 8 days. These methodologies were carried out in each of the coastal, dry, transition, and wet vegetation covers per island. Thus, the proportional sampling effort was similar between islands.

## Specimen analyses

A general description of the specimens found per species is provided. A total of ten linear measurements were taken (Table 1) from standardized photographs through the software ImageJ version 1.53p (Schneider et al. 2012). These measures were suggested in the literature for the separation of species of the genus (Papp 1999; Papp 2016; Mazhar et al. 2018). Specimens were identified to species using revisionary taxonomic keys provided by Papp (2010, 2016). Habitus images were taken with a digital camera Canon EOS 6D with an MPE-65 mm macro lens, attached to a CASTEL-MICRO Novoflex focusing rack stepping motor-controlled; Stacking was reached using the Helicon Focus software 8.2.2. and then edited using the Adobe Photoshop® CS6 v.13.0.

**Table 1.** Morphometric characters measured for the species of *Chelonus* of the Galapagos archipelago. In parentheses the abbreviations used for each variable.

| Measurements | Authors |
|---|---|
| Stigma width **(SW)** | Papp 2016 |
| Mesosoma length **(ML)** | Papp 1999 |
| Gena height **(GH)** | Mazhar et al. 2018 |
| Face length **(FL)** | Mazhar et al. 2018 |
| Clypeus length **(CL)** | Papp 2016 |
| Metasoma maximum width in lateral view **(MWL)** | Papp 1999 |
| Penultimate flagellomere length **(PFL)** | Papp 2016 |
| Metasoma maximum width in dorsal view **(MWD)** | Papp 2016; Mazhar et al. 2018 |
| Lateral ocellus diameter **(LOD)** | Mazhar et al. 2018 |
| Anterior ocellus diameter **(AOD)** | Mazhar et al. 2018 |

## Morphological differentiation of species between islands

Populations with more than five individuals from each island were included in statistical analyses. Cluster analysis with Euclidean distances and average clustering was used to visualize whether populations are structured, these groups are supported according to an approximately unbiased *P* value, that represents the support to these groups (Efron et al. 1996; Peña 2002). Cluster analysis was performed using the package PVCLUST of R (Suzuki and Shimodaira 2006). PerMANOVA test was used to know whether there are statistical differences between populations PerMANOVA was performed using the package VEGAN of R (Oksanen et al. 2022). Additionally, we applied the shape PCA and the PCA ratio spectrum analyses developed by Baur and Leuenberger (2011) to identify those ratios that discriminate between groups. The ratios came from the linear measurements.

## Morphological differentiation, island age, area, and distance between Islands

To study the relationship between morphological differentiation of the populations and area and age of the islands, we used the Mahalanobis distance between the

centroid of each cloud of individuals from each island and the centroid of all samples (Escobedo and Plata 2008). To study the relationship between morphological differentiation of the populations and the linear distances between islands, we used the Euclidean distance between the centroids of each pair of populations as this measure allows to determine how far two vectors are from each other (Shumskaya 2013). For all cases we used simple regression analyses. The ages of the islands were taken from Geist et al. (2014); the area of the islands and the distances between islands from Snell et al. (1996). Statistical analyses were conducted in the environment R 4.1.2 (R Core Team 2021). This protocol is available at DOI: https://dx.doi.org/10.17504/protocols.io.kxygxynmzl8j/v1.

# Results

## Species records

A total of seven chelonine species were identified from the Galapagos islands (Fig. 1): *Chelonus buscki* Viereck, 1912, *Chelonus carinatus* Provancher, 1881, *Chelonus johni* Marsh, 1979, *Chelonus refluus* (Papp, 2010), *Chelonus sulcifera* (Papp, 2016), *Chelonus topali* (Papp, 1999), and *Chelonus turgoclarus* (Papp, 2010). No endemic species were identified for the islands as in all cases these species have also been reported from other regions of the Neotropics.

*Chelonus turgoclarus* was found on almost all the islands, except for the Fernandina, Santa Cruz, and San Cristobal islands. *C. carinatus* was collected from Floreana, Santiago, San Cristobal, Santa Cruz, and Isabela islands. *C. topali* was collected from Floreana, Santiago, Santa Cruz, and Isabela islands. *C. buscki* was found on Floreana, Santiago, Pinta and Fernandina islands. *C. johni* was found in Floreana, Isabela and Santa Cruz. *C. sulcifera* and *C. refluus* were found in Floreana only.

The number of species per island was not related to the size of the islands. On Isabela (4588 km$^2$) four species were reported, on Fernandina (642 km$^2$) one species, on Santiago (584 km$^2$) four species, on San Cristobal (558 km$^2$) one species, on Floreana (172 km$^2$) seven species, on Española (60 km$^2$) one species, and on Pinta (59 km$^2$) two species.

## Key to *Chelonus* species known to occur in the Galapagos Islands

1 Frons laterally with a curved carina between lateral ocellus and compound eye ........ **2**

– Frons laterally lacking a curved carina between ocellus and eye ........ **5**

2(1) Apex of metasomal carapace in dorsal view with a pointed tip; (refluus species-group) ........ **3**

– Apex of metasomal carapace in dorsal view rounded or cup-shaped, not pointed ........ **4**

3 (2) Carapace in lateral view, deeply incurved ventrally; in ventral view, aperture of carapace shorter than carapace itself; apex of female carapace lacking a foramen ***Chelonus* (*Microchelonus*) *refluus* (Papp, 2010)**

– Carapace in lateral view apically truncate; in ventral view aperture of carapace nearly as long as carapace itself; apex of female carapace with a small round foramen .................................. ***Chelonus* (*Microchelonus*) *sulcifera* (Papp, 2016)**

4(2) Female carapace in lateral view 2.6–2.8× longer than high posteriorly; pterostigma 2.5–2.7× longer than wide...... ***Chelonus* (*Microchelonus*) *buscki* (Viereck, 1912)**

– Female carapace not so high posteriorly, in lateral view 4.4× longer than high posteriorly, 3.0× longer than wide in males; pterostigma 3.3–4.0× longer than wide; carapace either entirely black, or with small yellow spots, widely separated; male carapace with large wide apical foramen 3.0× wider than high laterally, foramen slightly narrowed medially................................................................ ................................***Chelonus* (*Microchelonus*) *carinatus* Provancher, 1881**

5(1) Face finely punctured but otherwise polished and shiny; female carapace in dorsal view somewhat globose, 1.6× as long as broad............................................ .................................... ***Chelonus* (*Microchelonus*) *turgoclarus* (Papp, 2010)**

– Face finely rugulose and dull; carapace longer and narrower; male carapace with a large oval apical foramen (as in Marsh 1979, Fig. 9)....................................7

6(5) Carapace in dorsal view 2.0× as long as broad, striated with numerous anastomoses......................................***Chelonus* (*Microchelonus*) *johni* Marsh, 1979**

– Carapace in dorsal view 1.7× as long as broad; undulate striated, interstriations rugulose................................ ***Chelonus* (*Microchelonus*) *topali* (Papp, 1999)**

## Diversity of *Chelonus* in the Galapagos archipelago

### ***Chelonus buscki* (Viereck, 1912)**

Fig. 1A

*Chelonus* (*Chelonella*) *buscki* Viereck, 1912: 618. Type locality: Montserrat, Trinidad.
*Microchelonus buscki* (Viereck): Shenefelt 1973: 878. Papp 2010: 157, 172. Papp 2016: 236–237.

**Description. Female.** Body length 2.12–2.80 mm. Head black; Mandibles yellow with basal and apical areas brown. Carinae between ocelli and eyes present. Antenna shorter than the body, penultimate flagellomere cuboidal. Scape yellow, pedicel concolorous with the scape. Flagellomeres brownish. Mesosoma black, scutellum rugose. Foreleg entirely yellow. Medial and hind legs as follows: coxa brown-black, trochanter yellow, femur mostly brown to black with proximal and distal apex turning yellow, medial tibia entirely yellow, hind tibia light-yellow with a brown medial macula. Medial and hind leg with tarsi 1–4 yellow, last tarsomere dark brown. Fore wing stigma brown. Metasoma black or brownish, without yellow maculae. In dorsal view basal part of metasoma without longitudinal carinae. Apical foramen of carapace present.

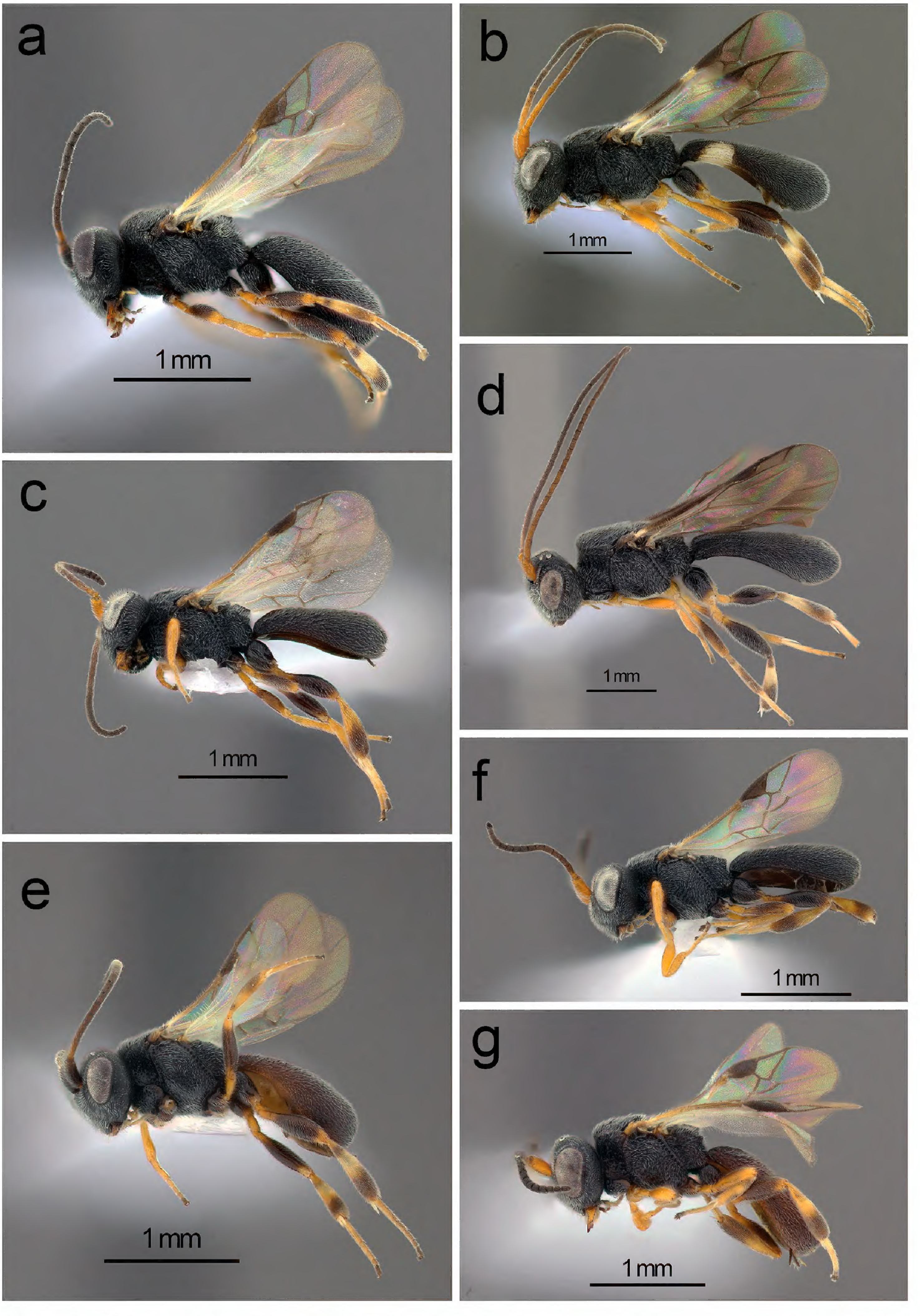


**Figure 1.** Habitus of the *Chelonus* species found in the Galapagos islands. *Chelonus buscki* **A** *Chelonus carinatus* **B** *Chelonus johni* **C** *Chelonus refluus* **D** *Chelonus sulcifera* **E** *Chelonus topali* **F** *Chelonus turgoclarus* **G**. Scale bars: 1 mm. All are females.

The specimens from Galapagos Archipelago did not show a pair of large yellow spots or a single pale-yellow band on its carapace as indicated in Viereck´s (1912) description. Instead, some specimens have a testaceous or dark brown irregular area as described above.

**Comments.** *C. buscki* is a very widespread and common neotropical species, having previously been recorded in Costa Rica, Honduras, Panama, Peru, and Trinidad (Papp 2016). This is the first record of the species in the Galapagos.

In Costa Rica, it has been reared from *Omiodes cuniculalis* (Crambidae) feeding on host plants including *Gliricidia sepium*, an introduced species of Fabaceae and other woody host plants (Sharkey et al. 2021). *C. buscki* is a species that is easily identified using Papp's (2016) key and comes out at couplet 42. A full morphological description is on pages 236–237 of Papp's (2016) revision.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 7 ♀♀; Cerro Pajas; 1°17'44.592"S, 90°27'29,447"W; 537 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; Humid zone; malaise trap; ECESPOCH - ICCDRS – **Fernandina** • 2 ♀♀; 0°21'50.076"S, 90°34'22.007"W; 1264 m a.s.l; 04–11 Nov. 2018; H. Herrera, J. Avendaño, P. Picón leg.; Humid zone; malaise trap; ECESPOCH - ICCDRS – **Santiago** • 2 ♀♀; 0°13'3.828"S, 90°43'27.84"W; 334 m a.s.l; 23–26 Jun. 2021;H. Herrera, J. Avendaño, P. Picón leg.; PanTrap; ECESPOCH - ICCDRS – **Pinta** • 5 ♀♀; 0°33'57.744"S, 90°45'14.435"W; 257 m a.s.l; 19–22 Jul. 2021; H. Herrera, J. Avendaño, P. Picón leg.; Humid zone; PanTrap; ECESPOCH - ICCDRS.

### *Chelonus carinatus* Provancher, 1881
Fig. 1B

*Chelonus carinatus* Provancher, 1881: 199. Type locality: Canada.
*Chelonus* (*Microchelonus*) *carinatus* (Provancher): McComb 1968: 5, 7, 34.
*Microchelonus carinatus* (Provancher): Shenefelt 1973: 878. Papp 1999: 189. Papp 2010: 175. Papp 2016: 243.

**Description. Female.** Body length 3.82–3.88 mm. Head black. Mandibles yellow with basal and apical areas brown. Antenna shorter than the body, penultimate flagellomere longer than wide. Scape yellow to brownish. First half of flagellomeres yellow to brownish. Carinae between ocelli and eyes present. Mesosoma black. Scutellum rugose. Foreleg: Coxa, femur, tibia and basal tarsomere brownish to yellow, trochanter light yellow, last tarsomere brownish to black. Middle leg: Coxa and trochanter brownish yellow, femur and tibia mostly brown to black with proximal and distal apex turning yellow, tarsi 1–4 yellow, last tarsomere black. Hind leg: Coxa black with apex yellow, Trochanter light yellow. Femur brown to black with proximal and distal apex turning yellow, tibia black to brownish with a proximal light-yellow band. Tarsi 1 to 3 mostly yellow, tarsi 4 and 5 brown. Fore wing stigma brown, veins RS, M, RSM and C+SCR light-yellow. Metasoma black with two lateral proximal yellow maculae, apical part also pale colored. Carapace in dorsal view with a pair of basomedially longitudinal carinae. Apical foramen of carapace absent.

**Comments.** *C. carinatus* has been recorded as occurring widely in Canada, USA (Florida), and Central America (Papp 2016). This is the first record of the species in the Galapagos. *C. carinatus* is distinguished by the carapace being long and narrow (0.4× as wide as long in dorsal view), wings strongly infumated, and mesoscutum with dense confluent punctation. The carapace sculpture dorsally is distinctively longitudinally rugulose. The specimens collected in Galapagos present the apical part of the carapace pale colored while the descriptions provided by McComb (1968) and Papp (2016) indicated this is entirely black.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 30 ♀♀; Cerro Pajas; 1°17'38.256"S, 90°27'27.396W; 580 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; Humid zone; malaise trap; ECESPOCH - ICCDRS – **Isabela** • 1 ♀; 0°50'44.736"S, 91°3'22.355"W; 527 m a.s.l; 05 Jun. 2019; J. Avendaño leg.; Humid zone; swp; ECESPOCH - ICCDRS – **Santiago** • 1 ♀; 0°11'33.396"S, 90°47'43.008"W;42 m a.s.l; 23–26 Jun. 2021; H. Herrera, J. Avendaño, P. Picón leg.; malaise trap; ECESPOCH - ICCDRS – **San Cristobal** • 4 ♀♀; 0°54'55.224"S, 89°26'2.184"W; 149 m a.s.l; 14–17 Jun. 2019; J. Avendaño, D. Albuja leg.; dry zone; PanTrap; ECESPOCH - ICCDRS – **Santa Cruz** • 1 ♀; 0°41'24.9"S, 90°13'18.804"W; 21 m a.s.l; 25 Sep.-02 Oct. 2018; J. Avendaño, Y. Campaña, P. Picón leg.; malaise trap; ECESPOCH - ICCDRS.

### ***Chelonus johni*** **Marsh, 1979**

Fig. 1C

*Chelonus* (*Microchelonus*) *johni* Marsh, 1979: 14. Type locality: Palmira, Colombia.
*Microchelonus johni* (Marsh): Papp 1999: 185, 191, 194. Papp 2016: 268–270.

**Description. Female.** Body length 2.10–2.47 mm. Head black. Mandible brownish basally turning yellow distally. Antenna shorter than the body, penultimate flagellomere cuboidal. Scape yellow to brownish, pedicel concolorous with the scape. First two flagellomeres dark yellow, others brownish. Carinae between ocelli absent. Mesosoma black, scutellum rugose. Foreleg yellow with coxa and last tarsomere brownish. Middle leg coxa brownish, trochanter yellow, femur brown to black with proximal and distal apex turning yellow. Tibia and tarsi 1–4 yellow, last tarsomere brown. Hind leg coxa brown, femur and tibia black to brownish with a proximal light-yellow band, tarsi 1–4 yellow, last tarsomere brown. Fore wing stigma brown. Metasoma completely black. Carapace in dorsal view without longitudinal carinae. Opening in ventral part of carapace almost as long as carapace. Apical foramen of carapace present. Marginal cell along wing margin ¾ as long as stigma.

**Comments.** *Chelonus johni* has previously been recorded as occurring in Colombia, Costa Rica, Mexico, and Honduras (Marsh 1979), where it has been reported as a beneficial species parasitizing the potato tuberworm (*Scrobipalpula* species) and similar pest Gelechiidae. This is the first record of this species occurring in the Galapagos.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 3 ♀♀; Cerro Pajas; 1°17'38.292"S, 90°27'27.432"W; 580 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; humid zone; malaise trap; ECESPOCH - ICCDRS – **Isabela** • 1 ♀; 0°50'19.248"S, 91°4'53.435"W; 762 m a.s.l; 03–10 Jun. 2019; H. Herrera, J. Avendaño, D. Albuja leg.; Humid zone; malaise trap; ECESPOCH - ICCDRS – **Santa Cruz** • 1 ♀; 0°41'25.26"S, 90°13'17.579"W; 20 m a.s.l; 25 Sep.-02 Oct. 2018; J. Avendaño, Y. Campaña, P. Picón leg.; dry zone; malaise trap; ECESPOCH - ICCDRS.

### *Chelonus refluus* (Papp, 2010)

Fig. 1D

*Microchelonus refluus* Papp, 2010:180. Papp 2016: 296. Type locality: Yoro, Honduras.

**Description. Male.** Body length 3.82–3.88 mm. Head black. Mandibles yellow with basal and apically area brown. Antenna shorter than the body, penultimate flagellomere longer than wide. Scape yellow to brownish, pedicel concolorous with scape. Flagellomeres 1–3 yellow to brownish, other flagellomeres brownish. Carinae between ocelli and eyes present. Mesosoma black. Scutellum rugose. Foreleg yellow with last tarsomere brown. Middle leg: Coxa and trochanter yellow, femur and tibia brown to black with proximal and distal apex turning yellow, Tarsi 1–4 yellow to brownish, last tarsomere brown. Hind leg: Coxa black with apex yellow, trochanter yellow, femur brown to black with a proximal light-yellow band, tibia black with a light-yellow medial band, Tarsi 1–4 yellow to brownish, last tarsomere brown. Fore wing stigma brown with distal half of submarginal, second submarginal, and marginal cells darker. Metasoma black. Carapace in dorsal view with a pair of basomedially longitudinal carinae. Opening in ventral part of carapace almost as long as carapace. Apical foramen of carapace absent.

The specimens from the Galapagos islands have a completely black carapace differing from the description.

**Comments.** *C. refluus* has previously been recorded from Honduras (Papp 2016). This is the first record of this species occurring in the Galapagos.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 14 ♂♂; Cerro Pajas; 1°17'36.42"S, 90°27'24.767"W; 576 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; humid zone; malaise trap; ECESPOCH - ICCDRS.

### *Chelonus sulcifera* (Papp, 2016)

Fig. 1E

*Microchelonus sulcifera* Papp, 2016: 303–305. Type locality: 20 km from Upala, Costa Rica.

**Description.** Female- Body length 2.00–2.46 mm. Head black. Mandibles yellow with basal and apical areas brown. Antenna shorter than the body, penultimate flagellomere cuboidal. Scape dark yellow. Flagellomeres brownish. Carinae between ocelli and eyes present or

absent. Mesosoma black, scutellum rugose. Foreleg yellow, last tarsomere brown. Middle leg: Coxa brownish, trochanter yellow, both, femur and tibia dark yellow with an extensive medial brown macula, tarsi 1–4 yellow to brownish, last tarsomere brownish. Hind leg: Coxa brown, trochanter dark yellow, femur brown to black with proximal and distal apex yellow, tibia light-yellow with a brown medial macula, tarsi 1–4 yellow to brownish, last tarsomere brownish. Metasoma brownish, without carinae in dorsal basal part. Opening in ventral part of carapace almost as long as carapace. Apical foramen of carapace present.

**Comments.** *C. sulcifera* was recorded from Costa Rica and Honduras (Papp 2016). This is the first record of the species in the Galapagos.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 4 ♀♀; Cerro Pajas; 1°17'36.42"S, 90°27'24.767"W; 576 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; humid zone; malaise trap; ECESPOCH - ICCDRS.

### ***Chelonus topali*** **(Papp, 1999)**
Fig. 1F

*Microchelonus topali* Papp, 1999: 192. Papp 2016: 305–307. Type locality: Rio Negro, Argentina.

**Description. Female.** Body length 2.05–2.31 mm. Head black. Mandibles brownish. Antenna shorter than the body, penultimate flagellomere cuboidal. Scape brownish to black. Pedicel concolorous with the scape. Flagellomeres brownish. Carinae between ocelli and eyes absent. Mesosoma black, scutellum punctuate. Leg coloration highly variable, Foreleg: Coxa and trochanter black or brown, femur extensively brown with apex light brown or entirely dark brown. Tibia dark brown, tarsi 1–4 brown last tarsomere black. Middle leg: coxa brownish, femur brown to black, tibia dark yellow with proximal and distal apex turning brown or entirely dark brown, tarsi 1–4 brown last tarsomere black. Hind leg: coxa black, femur brown to black, tibia light-yellow with a brown medial macula, tarsi 1–4 brown or entirely dark brown, last tarsomere brown or entirely dark brown. Fore wing stigma blackish. Metasoma completely black. Opening in ventral part of carapace almost as long as carapace. Carapace in dorsal view without longitudinal carinae. Apical foramen of carapace absent.

**Comments.** *Chelonus topali* was previously recorded only from Argentina (Papp 1999). This is the first record of this species occurring in the Galapagos.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 19 ♀♀; Cerro Pajas; 1°17'38.292"S, 90°27'27.432"W; 580 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; Humid zone; pantrap; ECESPOCH - ICCDRS – **Isabela** • 3 ♀♀; 0°50'19.248"S, 91°4' 53.435"W; 762 m a.s.l; 03–06 Jun. 2019; J. Avendaño, D. Albuja leg.; Humid zone; pantrap; ECESPOCH - ICCDRS – **Santiago** • 1 ♀; 0°12'1.62"S, 90°42'45.539"W; 98 m a.s.l; 23–26 Jun. 2021; H. Herrera, J. Avendaño, P. Picón leg.;malaise trap; ECESPOCH - ICCDRS – **Santa Cruz** • 1 ♀; 0°41'24.9"S, 90°13'18.804"W; 21 m a.s.l; 25 Sep.-02 Oct. 2018; J. Avendaño, Y. Campaña, P. Picón leg.; malaise trap; ECESPOCH - ICCDRS.

### *Chelonus turgoclarus* (Papp, 2010)
Fig. 1G

*Microchelonus turgoclarus* Papp, 2010: 186–189. Papp 2016: 309–311. Type locality: Pichin, Rio Pisque, Ecuador.

**Description. Female.** Body length 2.45–2.60 mm. Head black. Mandibles yellow and apically brown. Antenna shorter than the body, penultimate flagellomere cuboidal. Scape dark yellow. Pedicel and flagellomeres dark yellow to brown apically. Carinae between ocelli and eyes absent. Mesosoma black, scutellum rugose. Foreleg yellow. Last tarsomere brownish. Middle leg coxa brownish, trochanter yellow, femur extensively brown to black with proximal and distal apex turning yellow, tibia dark yellow with proximal and distal apex turning brown. Tarsi 1–4 yellow, last tarsomere 5. Hind leg: Coxa brown to black, trochanter dark yellow, femur mostly brown to black with proximal and distal apex yellow, tibia black with a light-yellow medial band, tarsi 1–4 yellow with the last tarsomere brown. Fore wing stigma brown. Metasoma black or brownish. Opening in ventral part of carapace almost as long as carapace. Carapace in dorsal view without longitudinal carinae. Apical foramen of carapace present.

**Comments.** *Chelonus turgoclarus* was previously recorded only from continental Ecuador (Papp 2010). This is the first record of this species occurring in the Galapagos.

**Specimens studied.** Ecuador, Galápagos – **Floreana** • 9 ♀♀; Cerro Pajas; 1°17'38.292"S, 90°27'27.432"W; 580 m a.s.l; 22–29 May. 2019; J. Avendaño, D. Albuja leg.; Humid zone; pantrap; ECESPOCH - ICCDRS – **Isabela** • 2 ♀♀; 0°50'19.248"S, 91°4'53.435"W; 762 m a.s.l; 03–06 Jun. 2019; J. Avendaño, D. Albuja leg.; Humid zone; malaise trap; ECESPOCH - ICCDRS – **Santiago** • 1 ♀; 0°13'43.932"S, 90°44'12.984"W; 543 m a.s.l; 23–26 Jun. 2021; H. Herrera, J. Avendaño, P. Picón leg.; malaise trap; ECESPOCH - ICCDRS – **Pinta** • 1 ♀; 0°34'0.804"N, 90°45'15.947"W; 264 m a.s.l; 19–22 Jun. 2021; H. Herrera, J. Avendaño, P. Picón leg.; malaise trap; ECESPOCH - ICCDRS – **Española** • 1 ♀; 2°0'56.304"S, 98°28'45.084"W; 135 m a.s.l; 03–06 Jul. 2021; J. Avendaño, P. Picón, G. Fiorentino leg.; malaise trap; ECESPOCH - ICCDRS.

## Morphological differentiation of populations between islands

Due to sample size, comparisons could only be made for the species *Chelonus buscki* from Floreana and Pinta islands, and for *Chelonus carinatus* from Floreana and San Cristobal islands. For *Chelonus buscki* the PCA showed no evident differentiation by island (Fig. 2A); the cluster analysis formed a single group with a support of 92% that excludes individuals 5, 7, and 9, the first one was collected in Floreana island and the last two from Pinta (Fig. 2B). However, differences for *C. buscki* between the population from Floreana and Pinta islands were identified with the PerMANOVA analysis ($F_{9,1}$ = 83.49, $P$ = 0.002) and these were consistent with the shape PCA (Fig. 3A). The PCA ratio spectrum shows that the two variables that explain most of the variation for

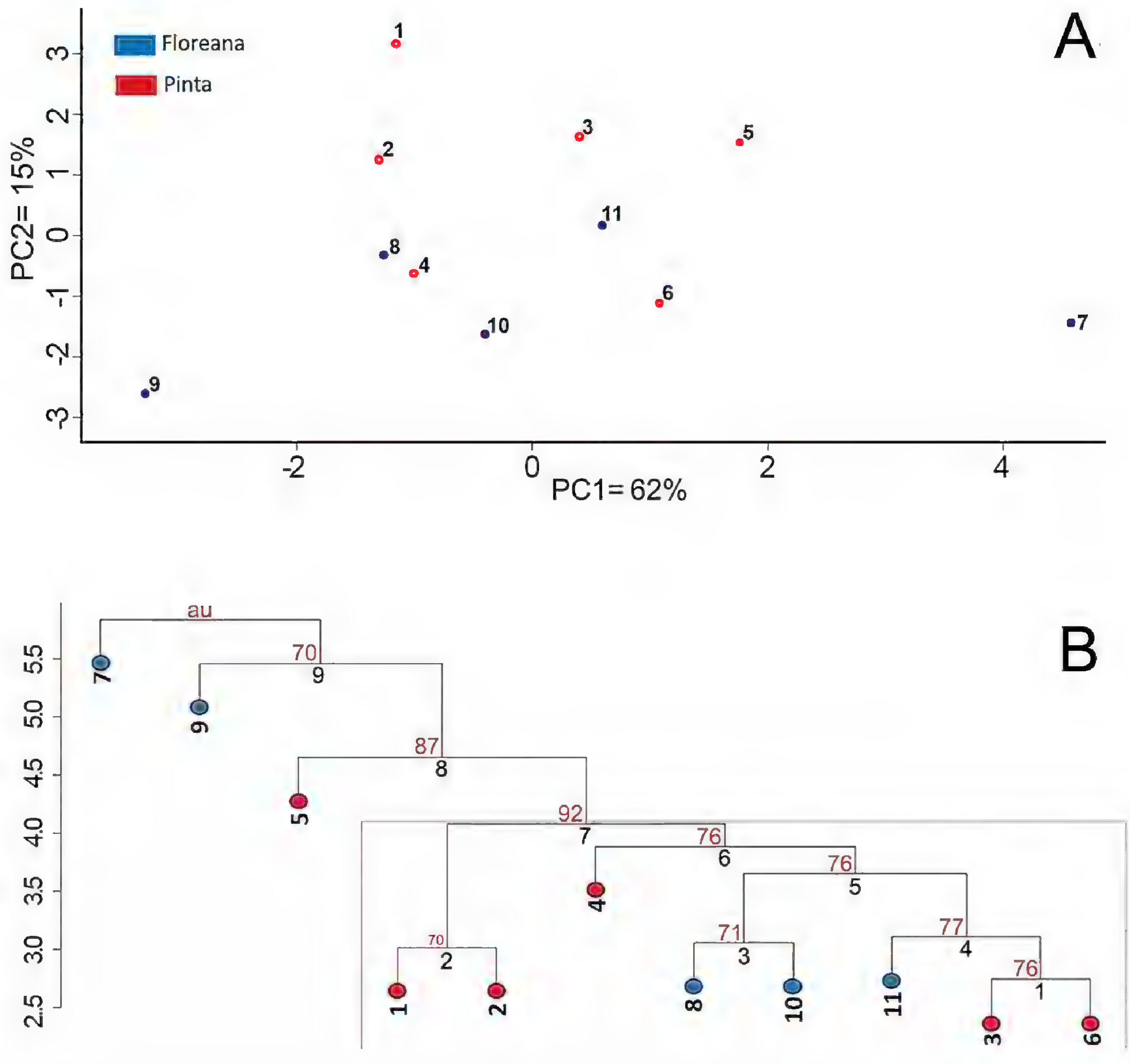


**Figure 2.** Projection of specimens of *Chelonus buscki* from Floreana and Pinta islands **A** PCA and **B** cluster analysis. Numbers by each circle refer to the individuals. Numbers above a group of individuals show approximate unbiased *P* support. The Frame encloses a group of individuals with 92% support.

the first component are Clypeus Length (CL) and Anterior Ocellus Diameter (AOD); for the second component they are the Penultimate Flagellomere Length (PFL) and the Lateral Ocellus Diameter (LOD) (Fig. 3B).

For *Chelonus carinatus* the PCA showed no evident differentiation by island (Fig. 4A); the cluster analysis yielded individuals 20 and 30 as highly differentiated, and two clusters, the large one contains a single subgroup with 99% support, and the small cluster with 99% support. None of the clusters include individuals of the same islands (Fig. 4B); this differentiation of the two clusters was supported by the PerMANOVA test ($F_{32,1}$ = 47.088, $P$ = 0.001). However, the scatterplot of the shape PCA formed two very clear groups composed of individuals of each island (Fig. 5A). The PCA ratio spectrum shows that the first component is mainly explained by the variables Penultimate Flagellomere Length (PFL) and Clypeus Length (CL) (Fig. 5B, left), while the second

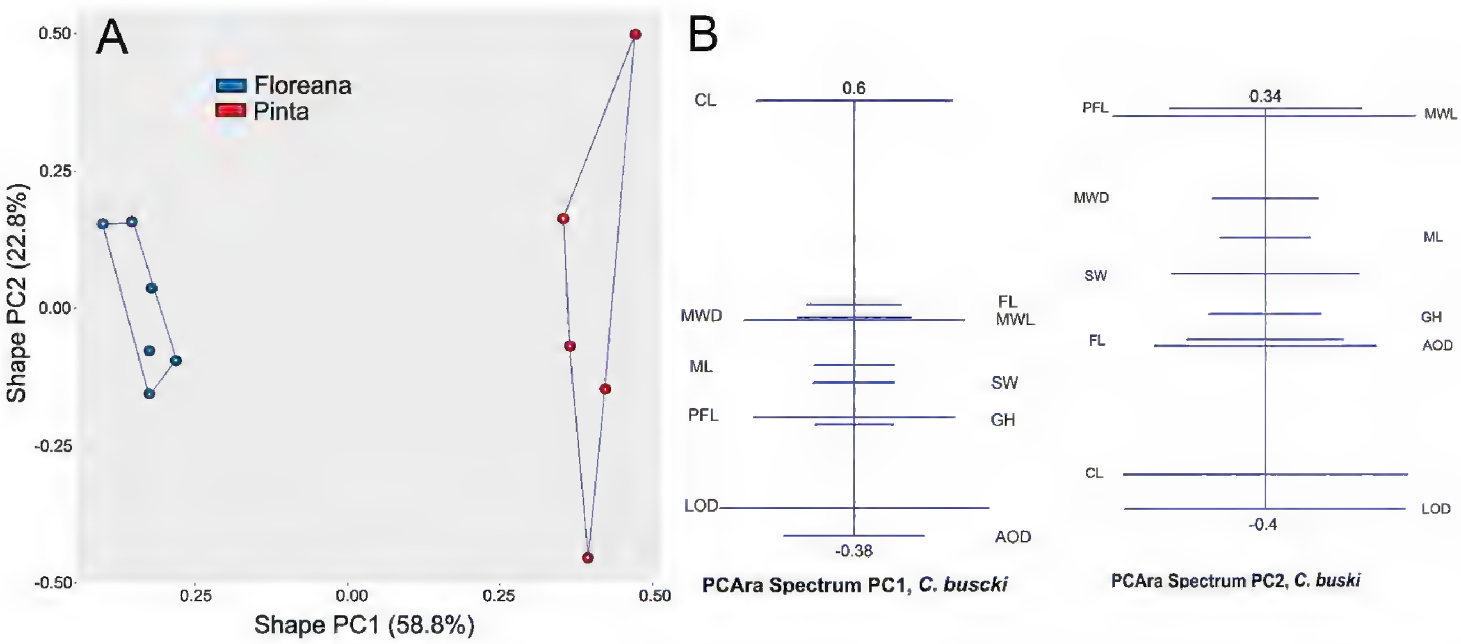


**Figure 3.** Projection of *Chelonus buscki* from Floreana and Pinta islands based on ratios **A** scatterplot of shape PCA, and **B** PCA ratio spectrum. The first component is displayed on the left, the second component on the right.

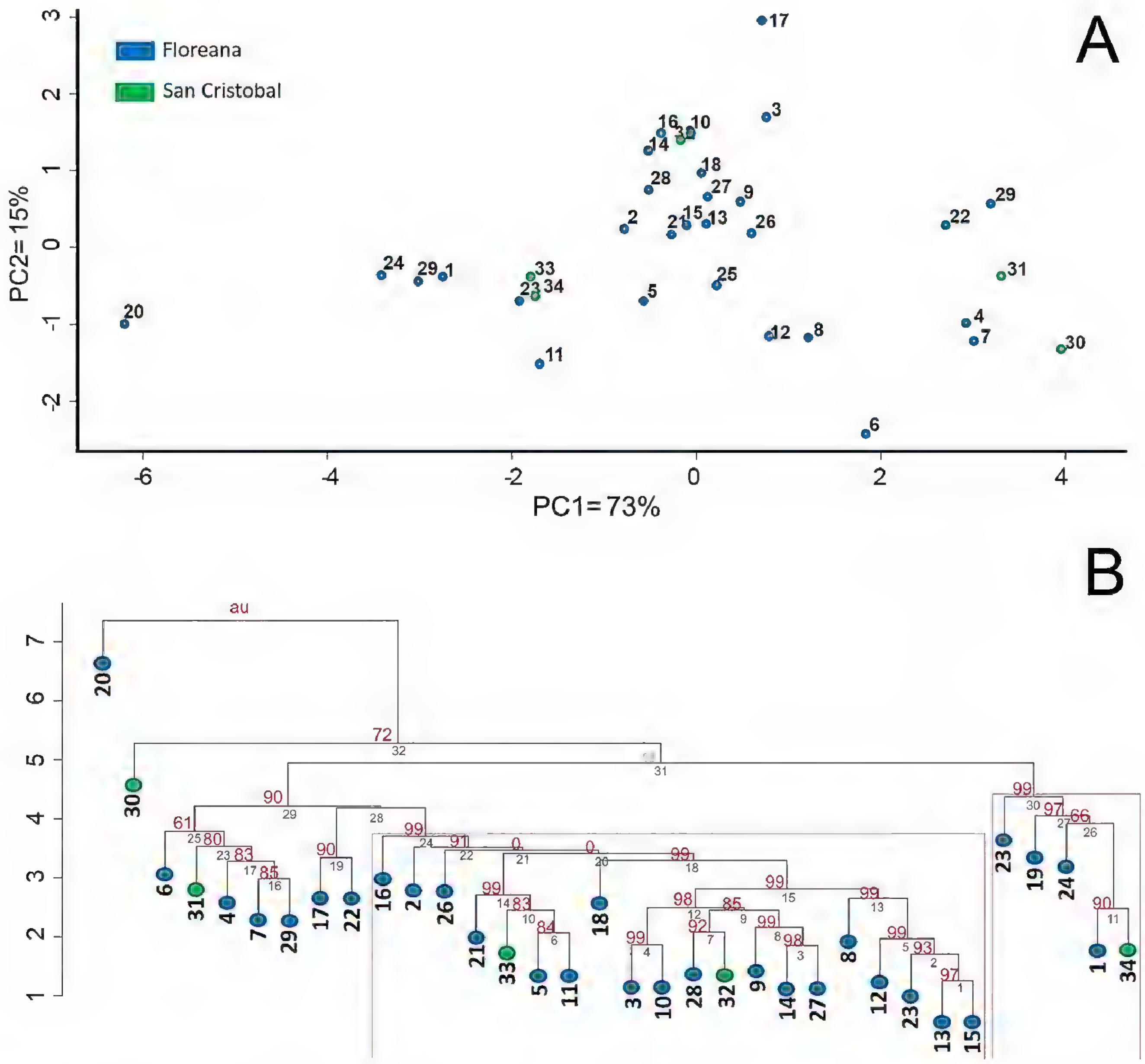


**Figure 4.** Projection of specimens of *Chelonus carinatus* from Floreana and San Cristobal islands **A** PCA and **B** cluster analysis. Numbers refer to the individuals. Frames enclose groups of individuals with 99% *P* support.

component is due to the combination of Penultimate Flagellomere Length (PFL) and Lateral Ocellus Diameter (LOD) (Fig. 5B, right). These differences between the PCA of the linear measurements and the shape PCA suggest a shape differentiation process.

Linear regression analyses showed a relationship between morphological differentiation and the area of islands for *C. buscki* only (Table 2, Fig. 6); No other variable or species appeared related (Table 2). *C. sulcifera*, *C. refluus*, and *C. johni* were not analyzed since they were present only on one island or were represented by only one or two individuals. For *C. buscki* we found that the larger the islands the smaller the differentiation between wasp populations for this species (Fig. 6).

## Discussion

The seven species found in the archipelago are first reports as no previous list of the Hymenoptera of the Galapagos included any reference to the group. *Chelonus* species were found on eight out of ten islands sampled. Larger islands are expected to support higher diversity (Gillespie and Roderick 2002) and this pattern has been reported for

**Table 2.** Linear regression analyses between morphological differentiation of *Chelonus* species and island traits. Morphological differentiation expressed as Mahalanobis distances. Significant regressions are indicated with an asterisk.

| Species | Island age | | Island distance | | Island area | |
|---|---|---|---|---|---|---|
| | $R^2$ | $p$ | $R^2$ | $p$ | $R^2$ | $p$ |
| *Chelonus buscki* | 0.36 | 0.39 | 0.55 | 0.08 | 0.95 | 0.01* |
| *Chelonus carinatus* | 0.01 | 0.84 | 0.003 | 0.87 | 0.33 | 0.30 |
| *Chelonus topali* | 0.01 | 0.84 | 0.57 | 0.08 | 0.11 | 0.66 |
| *Chelonus turgoclarus* | 0.07 | 0.65 | 0.11 | 0.33 | 0.05 | 0.76 |

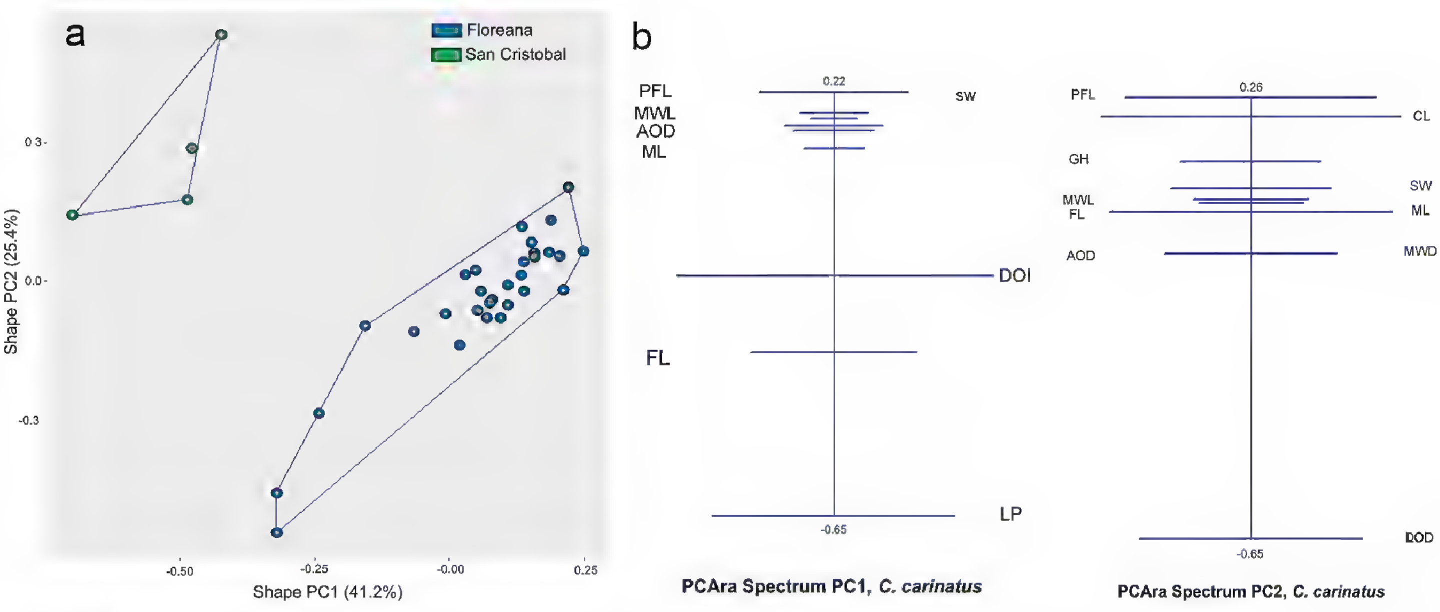


**Figure 5.** Projection of *Chelonus carinatus* from Floreana and San Cristobal islands based on ratios **A** scatterplot of shape PCA and **B** PCA ratio spectrum. The first component is displayed on the left, the second component on the right.

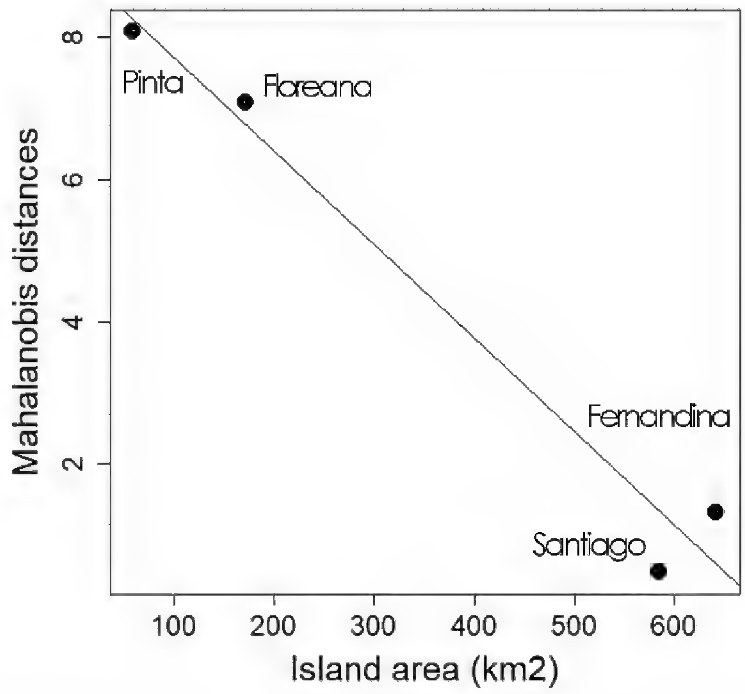


**Figure 6.** Plot of the relationship between morphologic differentiation of populations of *C. buscki* from each island and island area. This was the only statistically significant regression ($R^2$ = 0.95, F = 61.78, $p$ = 0.01).

the fauna of the Galapagos archipelago (Tye et al. 2002). However, this seem not the case of the species of *Chelonus*; on Isabela, the largest island, only four species of *Chelonus* were found, while on Floreana, the sixth largest, all seven species are reported. Probably due to the low number of species of the genus in Galapagos, this pattern was not observed, and the pattern is applicable to large number of species.

On the other hand, it is expected that isolation may facilitate modifications in morphology, behavior, and ecology, ranging from population incipient differentiation to a high frequency of endemism in oceanic islands (Roderick and Gillespie 1998), for example in the Galapagos, 47% of insects are endemic (Peck 1997; Peck et al. 1998). In contrast, all the *Chelonus* species are found elsewhere in the Neotropical or Nearctic regions. *C. buscki* is reported from Costa Rica, Honduras, Panama, and Peru. *C. carinatus* from Canada. *C. topali* from Argentina. *C. johni* is found in Colombia, Costa Rica, Honduras, and Mexico. *C. turgoclarus* is reported from continental Ecuador, in the Guayllabamba region, *C. sulcifera* is reported in Costa Rica and Honduras. These species may be part of the numerous entities that recently arrived at Galapagos. As Bulgarella et al. (2022) estimated, more than 500 species of insects have been introduced to the Archipelago.

The distance between islands is proposed as an important factor for differentiation and eventual speciation (Kellie et al. 2019), however, in our study no association was found between this characteristic and the morphological differentiation of the populations; this finding may result from a recent arrival to the archipelago as described above, although multiple studies have found that longer distances not always lead to larger differentiation; such as the case of populations of the lizards *Podarcis bocagei* and *P. hispanica* occurring in the Ria de Arousa archipelago in Spain, where differentiation does not agree with the distance between the islands (Arntezen and Sá-Sousa 2007). In our case, the only significant relationship was negative for *C. buscki* that may be a

consequence of a stronger founder effect of the few wasps in smaller island; further research may clear this preliminary result.

The ages of emergence and colonization time of islands can be related to the differentiation between populations (the progression rule) (Funk and Wagner 1995; Roderick and Gillespie 1998; Juan et al. 2000; Hormiga et al. 2003; Nepokroeff et al. 2003; Holland and Hadfield 2004; Cowie and Holland 2006; Illera et al. 2007). And some groups have shown a general agreement with the progression rule such as the moths of the genus *Galagete* (Schmitz et al. 2007). However, in our case, no association was found between the morphological differentiation of the populations of *Chelonus* species and the ages of the Galapagos islands. An interesting case that could shed light on what happened in *Chelonus* occurs with the subspecies of the bird *Parus caeruleus* from the Canary Islands archipelago; this species initially colonized Tenerife, the fifth oldest island, and later diversified in the archipelago without following a consistent pattern with the ages of the islands (Kvist et al. 2005).

There are other factors of population differentiation that could explain what was observed in *Chelonus* wasps. Selective pressures and local conditions, such as temperature, climate, predators (Chamberland et al. 2020; Mathys and Lockwood 2011), ocean currents and prevailing wind patterns can facilitate the use of islands to promote dispersal (Peake 1981; Ballard and Sytsma 2000; Hoskin 2000; Givnish and Renner 2004; Renner 2004; Cowie and Holland 2006). Several studies (Caccone et al. 2002; Sequeira et al. 2002; Torres-Carvajal et al. 2014) suggest that the colonization of the Galapagos Islands occurred thanks to the Humboldt current, which comes from the South American coast to the archipelago. In the case of the Fortuyniidae mites, they probably arrived due to the Panama Current that transports warm waters from Central America (Lea et al. 2006) and merges with the Peru Current until it reaches the archipelago (Pfingstl and Baumann 2017).

Finally, this work showed that the populations of a few species were morphologically differentiated between islands. Although it would be expected that these differences were associated with age, area, or geographic distance between islands, the results did not show this relationship for most of the species. This result could be a consequence of recent colonization events. As described in detail above, literature shows us that the predictions given by the models are not always fulfilled.

Our assumption about the progression rule has been fulfilled in archipelagos that have undergone geological processes of spatially and temporally ordered appearance of the islands; this is the case of the Hawaiian archipelago (Claridge et al. 2017). By contrast, the Galapagos archipelago has not had this spatial and temporal linearity, its islands have appeared in several island groups with strong variations in geographic distance and direction (Geist et al. 2014). Likewise, it would be unlikely that the progression rule would be fulfilled if the study taxon arrived long after the formation of the islands (Kvist et al. 2005). In our results, the *Chelonus* entities of the Galapagos archipelago are also found in the American continents, so most likely they arrived long after the Galapagos islands were already formed. Our results suggest that the group is recently established in the archipelago and its differentiation processes are very incipient.

## Conclusion

This study highlights the need for a more complete exploration of Galapagos fauna. *Chelonus* is a good example as the genus, with its seven new species here reported for the area, was not recorded in previous surveys despite being a common element in survey efforts. The genus appeared as a relatively recent arrival to the archipelago because no endemic species were identified for the islands and morphological differences were not associated with age or geographic distance between islands for any species.

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## Supplementary material 1

**Dataset *Chelonus* Galapagos**

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Data type: xlsx

Explanation note: The dataset contains a total of ten linear measurements of 114 individuals of the seven species of *Chelonus* reported for the Galapagos.



Link: https://doi.org/10.3897/jhr.97.130713.suppl1